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Changes in competitive ability between a C_4 crop and a C_3 weed with elevated carbon dioxide

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Using climate-controlled glasshouses, the growth of grain sorghum was evaluated with and without the presence of common cocklebur at current and projected future atmospheric concentrations of carbon dioxide [CO_2]. Single-leaf photosynthetic rates declined for both species in competition; however, elevated CO_2 reduced the percentage decline in common cocklebur and increased it in sorghum by 35 d after sowing (DAS) relative to ambient CO_2. In monoculture, elevated CO_2 significantly stimulated leaf photosynthetic rate, leaf area, and aboveground dry weight of common cocklebur more than that of sorghum. However, the stimulation of aboveground biomass or leaf area for monocultures of sorghum and common cocklebur at elevated CO_2 did not adequately predict the CO_2 response of aboveground biomass or leaf area for sorghum and common cocklebur grown in competitive mixtures. Overall, by 41 DAS, plant relative yield (PRY), in terms of aboveground biomass and leaf area, increased significantly for common cocklebur and decreased significantly for sorghum in competitive mixtures at elevated CO_2. Data from this study indicate that vegetative growth, competition, and potential yield of economically important C_4 crops could be reduced by co-occurring C_3 weeds as atmospheric carbon dioxide increases.

Nomenclature: Common cocklebur, *Xanthium strumarium* L. XANST; sorghum, *Sorghum bicolor* L. Moench.

Key words: Climate change, competition, XANST.

Because the C_4 photosynthetic pathway is overly represented in troublesome weedy species, many experiments and most reviews concerned with weed competition and rising CO_2 have reported on C_3 crop–C_4 weed interactions (Alberto et al. 1996; Patterson et al. 1984; Patterson 1986, 1993; Patterson and Flint 1990). Increasing CO_2 increased the crop–weed (i.e., the C_3/C_4) biomass ratio in all of these studies (see Bunce and Ziska 2000 for a review).

However, the idea that crops are fundamentally C_3 and weeds C_4, and that weed competition will consequently decrease as atmospheric CO_2 increases, should not be viewed as a universal axiom. Clearly, there are major C_4 crops of economic importance (e.g., corn [*Zea mays* L.], grain sorghum, pearl millet [*Pennisetum americanum* (L.) Leeke], sugarcane [*Saccharum officinarum* L.], and many important C_3 weeds (e.g., common lambsquarters [*Chenopodium album* L.], wild oat [*Avena fatua* L.], field bindweed [*Convolvulus arvensis* L.]. Crop–weed interactions vary significantly by region; consequently, depending on temperature, precipitation, soil etc., C_3 and C_4 crops may interact with C_3 and C_4 weeds (Bridges 1992).

At present, no data, other than the response of individual species, exist for the evaluation of competition between a C_4 crop and a co-occurring C_3 weed in response to atmospheric CO_2. Nevertheless, it is clear that the ongoing increase in atmospheric CO_2 may have important consequences for crop–weed competition and economic loss (Patterson 1995).

While comparisons of the response of individual C_3 weeds and C_4 crops could be extracted from the literature, it is unclear how well such comparisons predict competitive outcomes (Steinger et al. 1997). Consequently, the objective of the current study was to quantify CO_2-induced changes in competition between a C_4 crop, grain sorghum, and a co-occurring C_3 weed species, common cocklebur. Common cocklebur is listed as a troublesome weed for grain sorghum in nine states in the southern or central United States (Bridges 1992). "Troublesome" refers to weeds that result in a significant reduction in crop yield or quality (Bridges 1992).

Materials and Methods

The study was conducted in two climate-controlled glasshouses located at the USDA-ARS Climate Stress Laboratory in Beltsville, MD. Each glasshouse was 13.5 m^2 in surface area and transmitted 65% of incoming photosynthetically active radiation (PAR), with temperature and CO_2 concentration maintained within preset limits. Grain sorghum seed cv. 'Rio' and common cocklebur seed obtained commercially were sown in 20-cm-diameter plastic pots (11.5-L volume) in a 2 : 1 : 1 mixture of compost: jiffy mix[1] : perlite. The large pot size was used to avoid root binding effects. After sowing, the pots were watered to the drip point every other day. For all treatments, seed was thinned to establish a planting density of four plants per pot after emergence, either as a monoculture of sorghum or common cocklebur, or as a 50 : 50 mixture of sorghum and common cocklebur for each CO_2 treatment.

Because only two glasshouses were available, a randomized complete block design was used with runs over time as replications (blocks). For each run, four pots of each competitive treatment were randomly assigned to each of two benches within a glasshouse. For vegetative harvests, the mean value of eight pots of each competitive treatment was used as a single replicate. The entire experiment was run once in 1999, then repeated twice in 2000 for a total of three runs. CO_2 concentration treatments were switched between glasshouses twice during each run and between runs. Experiments were conducted from May through September. A two-way analysis of variance (ANOVA)[2] (CO_2 and competitive treatment as independent variables) was used to determine if the enhancement effect of elevated CO_2 differed between monoculture and mixture for a given species. Significant deviations of plant relative yield (PRY) from 1.0 at the 0.05 level as a function of CO_2 were determined with Student's t test assuming unequal variances. The effect of CO_2 was determined as the ratio of a measured variable at elevated CO_2 relative to that at ambient CO_2. Unless otherwise stated, differences were determined to be significant at the $P < 0.05$ level.

Glasshouses were set to maintain temperatures between a maximum and a minimum of 31 and 17 C, respectively. Air temperature was obtained by shielded, aspirated thermocouples near the top of plants in each glasshouse. PAR sensors were located near the top of each glasshouse. Dewpoint temperatures were determined periodically near midday and closely approximated those of outside air. Carbon dioxide was maintained by WMA2 infrared gas analyzers,[3] which injected CO_2 if levels fell below 350 and 700 μmol mol^{-1}, respectively, for each glasshouse. Blowers constantly circulated air through heat exchangers and produced an air speed of about 0.5 ms^{-1} across leaves. No significant differences with respect to PAR or temperature were observed between glasshouses. A datalogger[4] recorded PAR, temperature, and CO_2 concentration in both glasshouses at 30-s intervals. Average 24-h values of CO_2 were 410 $\pm$ 21 and 708 $\pm$ 36 μmol mol^{-1} for the ambient and elevated treatments, respectively. Because early vegetative growth, particularly leaf area, is a key determinant of competition (Kropff and Spitters 1991), 31 and again 41 d after sowing (DAS), two plants per pot (i.e., one each of common cocklebur : common cocklebur, common cocklebur : sorghum or sorghum : sorghum) were cut at ground level and separated into leaf laminae and stems (sheaths for sorghum). Leaf area was determined photometrically with a leaf area meter[5]. Dry weights were obtained separately for leaves and stems. Material was dried at 55 C for a minimum of 72 h (or until dry weight was constant) and weighed. Although roots were not separated between species, visual inspection of roots 41 DAS did not indicate that the plants were potbound. PRYs were calculated for aboveground biomass and leaf area according to the methods of Trenbath (1974) and Patterson et al. (1984) 31 and 41 DAS. In its simplest form, the PRY of species A in competition with species B is the dry weight (or other growth parameter) per plant of A grown in mixture with B (AB) divided by the dry weight when grown in monoculture (A from AA). Similarly, the PRY of species B is the dry weight of B from AB divided by the dry weight of B from BB. The relative competitiveness of A and B can then be estimated by comparing their PRY values in competition with each other (i.e., if the PRY of A > PRY of B, A is a more effective competitor, but if the PRY $\sim$1, then competition is balanced). In addition, if a treatment variable (e.g., CO_2) changes, its effect on the competitiveness of a given species can be assessed using PRY (see Patterson 1985 for a complete discussion).

At 20 and again at 35 DAS, single-leaf photosynthesis (determined as A, the rate of CO_2 assimilation) was measured for each species and treatment. On each sampling date, assimilation was determined on the uppermost, fully expanded leaf for six plants of each treatment. Measurements were made using a portable open-gas exchange system[6] incorporating infrared CO_2 and water vapor analyzers for determining net photosynthetic CO_2 uptake rate and stomatal conductance. Measurements were made using full sunlight (1,200–1,400 PAR). Water vapor surrounding the leaf ranged from 1.5 to 2.0 kPa and did not vary between CO_2 treatments. Comparisons between the short-term response of assimilation rate of leaves grown at ambient CO_2 to elevated CO_2 and the rates of leaves grown and measured at the elevated CO_2 concentration (i.e., long-term) were used to determine the extent of photosynthetic acclimation or "downregulation" over time for each species and competitive environment. Measurements of gas exchange were made during runs 2 and 3.

Results and Discussion

Ongoing increases in atmospheric carbon dioxide should stimulate leaf photosynthesis in C_3 plants by increasing the CO_2 concentration gradient from air to the leaf interior and by decreasing the loss of CO_2 via photorespiration. Alternatively, plants with the C_4 photosynthetic pathway already have an internal biochemical pump for concentrating CO_2 at the site of carboxylation that functions to eliminate the oxygenase component of Rubisco, thereby eliminating photorespiratory carbon loss. Because of these different photosynthetic pathways, it is anticipated that C_4 plants should be saturated at the current atmospheric CO_2 concentration, whereas C_3 plants should continue to respond photosynthetically to the ongoing increase in atmospheric CO_2.

The differential responses of C_3 and C_4 plants to increasing CO_2 are especially relevant to crop–weed competition in agro-ecosystems. Most crops are C_3 plants. Of the 15 crops that supply 90% of the world's calories, 12 are C_3 plants (Harlan 1975). Conversely, 14 of the 18 "world's worst weeds" are C_4 plants (Holm et al. 1977). As a consequence, most studies that have examined crop–weed competition at elevated CO_2 have done so for C_3 crop–C_4 weed mixtures (Bunce 1993; Carter and Peterson 1983; Newton et al. 1996; Patterson et al. 1984). In these studies, competitive ability of the C_3 crop was enhanced with elevated CO_2. As a consequence, Patterson (1995) suggested that crop losses due to weed competition may decline with the rise in atmospheric CO_2.

Prior to this study, however, no information was available on how C_4 crops would interact with C_3 weeds in a future, higher CO_2 environment, even though many C_3 weeds are considered troublesome in C_4 crops (e.g., velvetleaf [*Abutilon theophrasti*], common lambsquarters, and Canada thistle [*Cirsium arvense* (L.) Scop.] in corn and *Xanthium* spp. in sorghum, Bridges 1992). In a C_4 crop–C_3 weed mixture, does rising CO_2 still favor the crop?

In the current study, elevated CO_2 significantly increased single-leaf photosynthesis of common cocklebur in monoculture and in a sorghum : common cocklebur mixture (Ta-

TABLE 1. Leaf photosynthetic rate (determined as assimilation of CO_2 per unit leaf area per unit time) for cocklebur and sorghum growing in monoculture or in competitive mixtures at ambient (Amb.) and elevated (Elev.) carbon dioxide. Measurement concentration represents a short-term (minutes) exposure to elevated CO_2. Average 24-h values of [CO_2] were 410 ± 21 and 708 ± 36 μmol mol^{-1} ± SE for the ambient and elevated treatments, respectively.

Species	Competitor	DAS	[CO_2] (Grown/Measured) Amb./Amb.	Amb./Elev.	Elev./Elev.
			μmol m^{-2} s^{-1}		
Cocklebur	Cocklebur	20	42.6 ± 0.9	56.0 ± 1.0 A[a]	49.8 ± 4.3[a]
	Sorghum	20	40.7 ± 0.8	49.5 ± 1.7 B[a]	48.1 ± 1.0[a]
Cocklebur	Cocklebur	35	28.8 ± 1.7 A	49.7 ± 2.8[a]	44.3 ± 1.5[a]
	Sorghum	35	22.2 ± 2.8 B	42.6 ± 3.9[a]	41.1 ± 1.6[a]
Sorghum	Sorghum	20	40.3 ± 1.9	43.4 ± 1.4	42.1 ± 2.4
	Cocklebur	20	40.4 ± 1.2	47.4 ± 1.8[a]	37.5 ± 3.1
Sorghum	Sorghum	35	32.3 ± 1.3	37.8 ± 3.2	40.1 ± 1.5 A[a]
	Cocklebur	35	31.2 ± 2.4	34.3 ± 2.1	34.2 ± 2.4 B

[a] Indicates a significant increase in short- or long-term exposure to elevated CO_2 relative to ambient CO_2 (one-way ANOVA) for each row. Different letters indicate a significant difference in the response to [CO_2] as a function of competitive treatment (monoculture or competitive mixture) at a given sampling date with either short- or long-term exposure to elevated CO_2 (two-way ANOVA using competitive treatment [monoculture or 50 : 50 mixture] and CO_2, ambient or elevated, as independent variables for a given sampling date). DAS, days after sowing.

ble 1). For common cocklebur leaves grown at ambient CO_2, no significant difference in the degree of photosynthetic stimulation was observed between the short-term response of assimilation rate for leaves at elevated CO_2 and the rates of leaves grown and measured at the elevated CO_2 concentration (Table 1). This indicated no photosynthetic acclimation or down regulation for common cocklebur over the course of the experiment. In addition, the relative degree of stimulation for common cocklebur at elevated CO_2 increased from 20 to 35 DAS (Table 1) due to a greater reduction in photosynthetic rate over time for leaves grown at ambient CO_2. For the crop species, sorghum, no stimulation of single-leaf photosynthesis by elevated CO_2 was observed in monoculture 20 DAS, but significant photosynthetic stimulation was observed 35 DAS. However, the overall stimulation by elevated CO_2 was less than that observed for common cocklebur.

Consistent with the observed stimulation of photosynthetic rates, significant increases in stem weight and leaf weight were observed for the C_3 weed at elevated relative to ambient CO_2 both in monoculture and in mixture 31 and 41 DAS (Table 2). Stem weight increased to a greater extent than leaf weight, with a greater relative stimulation observed 31 vs. 41 DAS (63 vs. 31% for common cocklebur in monoculture 31 and 41 DAS, respectively). Significant stimulation of leaf area for common cocklebur was observed in monoculture and mixture 31 DAS and in competitive mixtures 41 DAS at elevated CO_2. For sorghum, elevated CO_2 did not stimulate stem weight, leaf weight, or leaf area at either sampling date (Table 2). However, a significant re-

TABLE 2. Stem weight, leaf weight, and leaf area (per plant) for cocklebur and sorghum in response to elevated carbon dioxide at 31 and again at 41 DAS.

CO_2	Species	Competitor	Stem wt.	Leaf wt.	Leaf area
			g	g	cm^2
31 DAS					
Ambient	Cocklebur	Cocklebur	1.42	2.24	621
	Cocklebur	Sorghum	1.20	2.36	572
Elevated	Cocklebur	Cocklebur	2.31[a]	3.34[a]	838[a]
	Cocklebur	Sorghum	2.36[a]	3.06[a]	795[a]
Ambient	Sorghum	Sorghum	1.45	2.15	774
	Sorghum	Cocklebur	1.44	2.08	770
Elevated	Sorghum	Sorghum	1.41	2.16	793
	Sorghum	Cocklebur	1.57	2.33	797
41 DAS					
Ambient	Cocklebur	Cocklebur	5.33	5.55	1,050
	Cocklebur	Sorghum	5.13	5.15	1,079
Elevated	Cocklebur	Cocklebur	6.97 B[a]	6.43[a]	1,234
	Cocklebur	Sorghum	9.67 A[a]	7.35[a]	1,382[a]
Ambient	Sorghum	Sorghum	7.78	9.71	2,004
	Sorghum	Cocklebur	7.67	8.30	1,943
Elevated	Sorghum	Sorghum	9.25	8.97 A	2,015 A
	Sorghum	Cocklebur	8.05	7.06 B	1,625 B[a]

[a] Indicates a significant effect of elevated CO_2 concentration for a given sampling date (one-way ANOVA). Different letters indicate a significant difference in the response to elevated [CO_2] as a function of competition (i.e., two-way ANOVA using competitive treatment, [monoculture or 50 : 50 mixture] and [CO_2], ambient or elevated, as independent variables for a given sampling date). DAS, days after sowing.

duction in leaf area was observed for sorghum in a sorghum : common cocklebur mixture 41 DAS with elevated CO_2.

For cocklebur and sorghum in monoculture, the relative stimulation of photosynthesis and biomass by elevated CO_2 is consistent with the published response of other species with the C_3 and C_4 photosynthetic pathway (Poorter 1993; Ziska and Bunce 1997). But if C_3 species always respond to a greater extent than C_4 species with increasing CO_2, why can't crop–weed competition be predicted solely as a function of pathway? Are competition experiments for species with different photosynthetic pathways even necessary at elevated CO_2? Indeed, many studies in which individual weed and crop species have been included in the same CO_2 treatments have been interpreted in terms of C_3 and C_4 competition, even though the plants did not compete directly. For example, weed : crop biomass ratios were reported to decrease at elevated CO_2 in comparisons of itchgrass [*Rottboellia cochinchinensis* (Lour.) W. Clayton] (C_4) with soybean [*Glycine max* (L.) Merr.] (C_3) (Patterson and Flint 1980), as well as in comparisons of barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.], goosegrass [*Eleusine indica* (L.) Gaertn.], and southern crabgrass [*Digitaria ciliaris* (Retz.) Koel.] (all C_4) with soybean (Patterson 1986).

However, although the response of C_3 species clearly differs from that of C_4 species, comparison of responses in monoculture may be a poor predictor of competitive outcomes when species are grown together at elevated CO_2. Competition per se may alter the relative stimulation of photosynthesis by elevated CO_2. For sorghum in the current study, the percentage decline was significantly different from 0 only at elevated CO_2 for 35 DAS; conversely, common cocklebur 35 DAS showed a significant decline at ambient, but not elevated, CO_2 (Table 1). Overall, the decline in photosynthesis with competition was altered by CO_2, with a greater reduction observed at ambient CO_2 for common cocklebur relative to sorghum and a greater reduction observed at elevated CO_2 for sorghum relative to common cocklebur (Table 1).

Competition may also alter the vegetative response to elevated CO_2. For example, the relative stimulation of aboveground biomass was significantly greater for common cocklebur when grown in common cocklebur : sorghum mixtures compared to monoculture at elevated CO_2 41 DAS (Figure 1). A slight but significant stimulation in aboveground biomass was observed for sorghum in a sorghum : common cocklebur mixture 31 DAS with elevated CO_2 (Figure 1). By 41 DAS, a significant reduction in leaf weight (and no change in aboveground biomass) was observed, however, for sorghum at elevated CO_2 in a sorghum : common cocklebur mixture (Table 2; Figure 1). Moreover, a significant depression in leaf area by elevated CO_2 was observed 41 DAS for sorghum in competition with common cocklebur (Figure 2). For common cocklebur, significant stimulation of leaf area by elevated CO_2 was also observed for both monoculture and mixture 31 DAS, but only in competitive mixtures 41 DAS (Table 2; Figure 2). No significant stimulation of leaf area by elevated CO_2 was observed for sorghum at either sampling date. Overall, 41 DAS, the ratio of leaf area of sorghum to cocklebur in monoculture was reduced by elevated CO_2 from 1.9 to 1.6. In mixture, however, elevated CO_2 reduced the ratio of leaf area of sorghum to common cocklebur from 1.80 to 1.18. Similarly, the ratio of aboveground biomass of sorghum to common cocklebur was reduced by elevated CO_2 from 1.6 to 1.4 in monoculture, but from 1.6 to 0.9 in competitive mixtures.

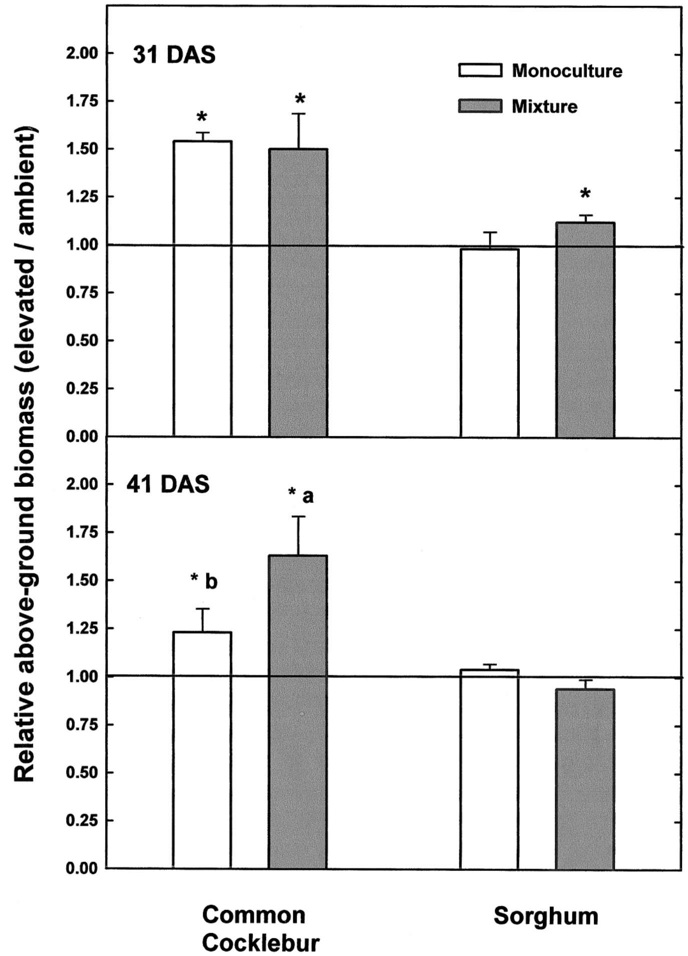

FIGURE 1. Aboveground biomass at elevated CO_2 relative to ambient CO_2, 31 and 41 d after sowing (DAS) for common cocklebur and sorghum grown at a ratio of 50 : 50 and common cocklebur and sorghum grown in monoculture; a value of one indicates no effect of CO_2. * indicates a significant difference relative to 1.0, $P < 0.05$, Students t test, assuming unequal variances. Different letters indicate a significant effect of competition relative to monoculture (two-way ANOVA using competitive treatment [monoculture or 50 : 50 mixture] and CO_2 [ambient or elevated] as independent variables for a given sampling date). See Methods for additional details. Average 24-h values of CO_2 were 410 ± 21 and 708 ± 36 μmol mol^{-1} ± standard deviation for the ambient and elevated treatments, respectively.

Overall, how is competitive ability affected by elevated CO_2? In the current experiment, based on aboveground biomass, the PRYs of common cocklebur and sorghum were approximately equal at ambient CO_2. However, the PRY of common cocklebur increased and the PRY of sorghum decreased, relative to a value of one (i.e., no effect of competition) 41 DAS with elevated CO_2 (Table 3). A similar pattern was observed for PRY based on leaf area 41 DAS (Table 3). Although the influence of elevated CO_2 on PRY has not been examined previously for C_4 crops and C_3 weeds in competition, other work by Bazzaz and Carlson (1984); Bazzaz and Garbutt (1988); Bazzaz et al. (1995); and Steinger et al. (1997) also found little relationship between the

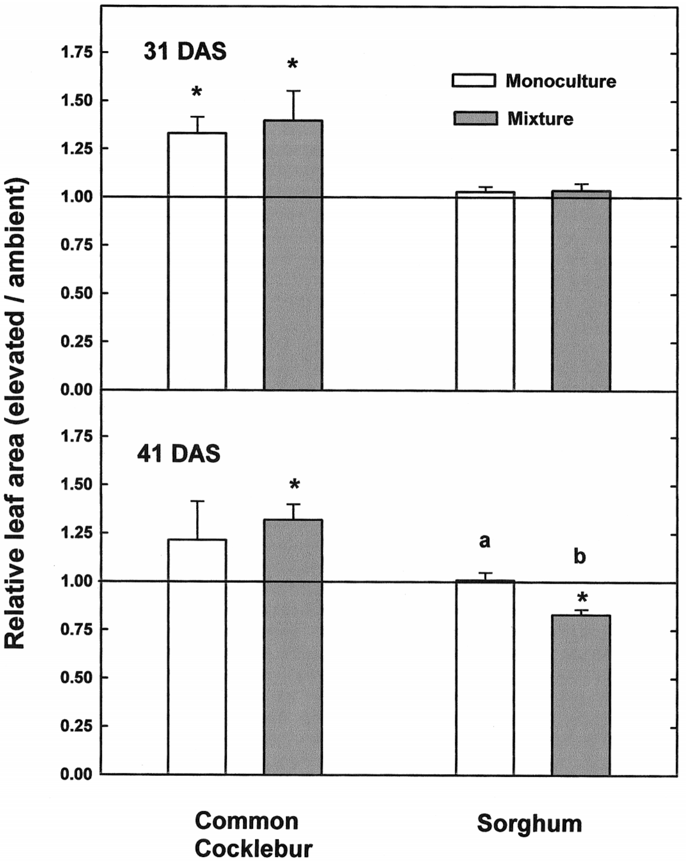

FIGURE 2. Leaf area at elevated CO_2 relative to ambient CO_2 31 and 41 d after sowing (DAS) for common cocklebur and sorghum grown at a ratio of 50 : 50 and common cocklebur and sorghum grown in monoculture; a value of one indicates no effect of CO_2. * indicates a significant difference relative to 1.0, $P < 0.05$, Student, t test, assuming unequal variances. Different letters indicate a significant effect of competition relative to monoculture (two-way ANOVA using competitive treatment [monoculture or 50 : 50 mixture] and CO_2 [ambient or elevated] as independent variables for a given sampling date). See Methods for additional details. Average 24-h values of CO_2 were 410 ± 21 and 708 ± 36 μmol mol^{-1} $\pm$ standard deviation for the ambient and elevated treatments, respectively.

relative responses of isolated and competing plants in response to elevated CO_2.

In the current study, the effect of competition was to enhance the relative response of cocklebur to elevated CO_2. Because competitive outcomes are often decided early in the growing season as a function of the relative ratio of crop to weed leaf area (Kropff and Spitters 1991), data from the current experiment would suggest a greater yield loss of sorghum with co-occurring common cocklebur in a future, higher CO_2 scenario.

While it is clear that future increases in atmospheric CO_2 are likely to affect crop–weed competition, the scope of the present experiment is limited to a single crop–weed pair under controlled conditions. To date, the majority of data concerning crop–weed interactions with increasing CO_2 and changing climate are based on studies in controlled-environment chambers or glasshouses. Almost no information is available on how long-term exposure to CO_2 per se or in conjunction with other environmental changes (e.g., water, temperature, and nutrients) will affect crop–weed interactions in situ. However, because of the overrepresentation of troublesome C_4 weeds, modeling efforts to assess the effects

TABLE 3. Plant relative yield (PRY) for cocklebur and sorghum grown at two levels of carbon dioxide, ambient and elevated at 31 and 41 days after sowing (DAS). PRY was calculated for both aboveground biomass and leaf area per plant as a function of CO_2 treatment.

DAS	Species	Ambient	Elevated
Aboveground biomass			
31	Cocklebur	0.95	0.96
	Sorghum	0.96	1.08
41	Cocklebur	1.02	1.29[a]
	Sorghum	0.92	0.84[a]
Leaf area			
31	Cocklebur	0.95	1.04
	Sorghum	0.98	0.96
41	Cocklebur	1.05	1.15[a]
	Sorghum	0.97	0.80[a]

[a] Indicates a significant difference in PRY for a given sampling date and species relative to a ratio of one (i.e., equal competitive ability) (Student's *t* test, assuming unequal variances). See Methods for additional details.

of weeds on crop production (see Chapter 4, Rosenzweig and Hillel 1998) may assume less yield loss due to weedy competition as atmospheric CO_2 increases. Although the current experiment is limited in scope, it does suggest that: (1) predicting competitive outcomes based on species grown in isolation may not adequately quantify crop–weed competition as a function of increasing CO_2, and (2) additional decreases in C_4 crop production could be expected from C_3 weeds with future increases in atmospheric CO_2.

Sources of Materials

[1] Jiffy mix, Jiffy Products, 951 Seanson Drive, Batavia, IL 60510.
[2] Statview, SAS Institute, Cary, NC 27513.
[3] Infrared gas analyzer, PP Systems, 241 Winter Street, Haverhill, MA 01830.
[4] Datalogger, 21x, Campbell Scientific, 815 West 1800 North, Logan, UT 84321.
[5] Leaf area meter, model 3100, Li-Cor Corporation, Lincoln, NE 68504.
[6] CIRAS-1, PP Systems, 241 Winter Street, Haverhill, MA 01830.

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